Effect of incubation temperature on growth performance in Atlantic salmon

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ABSTRACT: Interspecific variations in thermal growth performance of ectotherms have received considerable recent interest fueled by the focus on ecological climate change effects. Among-population variations in growth are commonly observed in field studies. However, the role of phenotypic plasticity in shaping this variation is largely unexplored in teleost fishes. Here, we tested for the effect of incubation temperature on thermal scaling of growth and maximum growth performance of the anadromous salmonid Atlantic salmon *Salmo salar* L. Salmon eggs were incubated and reared until the onset of exogenous feeding at either heated or natural temperatures or transferred from natural to heated temperatures at the time of hatching, creating 3 different embryonic temperature treatments (heated, natural or mixed). We subsequently tested for juvenile growth performance of these groups at 8 temperatures ranging from 6 to 24°C. Maximum growth was significantly higher in the heated than the natural and mixed incubation temperature groups, but we did not observe differences in the thermal scaling of growth performance. Neither the upper nor lower thermal limit for growth nor the optimal growth temperature differed between the 3 incubation temperature treatments. However, thermal conditions experienced by incubating embryos affected later growth performance. Although similar results have been observed previously among reptiles, this is to our knowledge the first empirical support for this hypothesis among teleost fishes. Phenotypic plasticity in growth performance can likely explain many of the contrasting findings from previous research on countergradient growth effects in teleost fishes.

KEY WORDS: Countergradient variation · Growth reaction norms · *Salmo salar* L. · Thermal adaptation · Thermal performance

INTRODUCTION

Temperature is perhaps the most important abiotic factor influencing individual growth rates of ectotherms (Ayrinhac et al. 2004, Castañeda et al. 2004) and a significant ecological factor for the evolutionary success of organisms (Hoffmann & Sgrò 2011). Populations are expected to adapt to local thermal conditions, and the function between individual growth rate and temperature increases to an optimum value and then decreases at higher temperatures (Elliott 1994). This function allows ectotherms to maintain thermal homeostasis within a wide range of temperatures (Angilletta et al. 2002). Furthermore, it influences the geographic range of species and affects how these will respond to rapid climate change (Angert et al. 2011, Finstad et al. 2011). However, the thermal performance curve may not be species specific but may vary among conspecific populations (Heilmayer et al. 2004), making thermal responses to climatic variation more difficult to predict (Schulte et al. 2011).

Intraspecific variation in thermal performance has caused considerable ecological debate (Jonsson & Jonsson 2011) and given rise to at least 3 different hypotheses to explain this variation: (1) Growth rate

is adapted to local thermal optima (Levinton 1983, Stillwell & Fox 2005). This implies that variation in growth rate reflects thermal adaptation to conditions in the home environment. Natural selection is then expected to shift the optimum temperature for growth to match the prevailing temperature in a new or changed thermal regime. (2) Growth rate is higher for populations adapted under hostile environmental conditions (e.g. cold habitats, short season for growth, strong competition for food) than those which have evolved under benign conditions (countergradient hypothesis, Levins 1969, Conover & Schultz 1995). (3) Thermal conditions experienced by embryos during incubation affect later growth performance (Scheiner 1993, Qualls & Andrews 1999, Andrews 2008). This latter relationship has been reported in studies of turtles, lizards and crocodilians but is less well known in other vertebrate groups such as teleost fishes (Booth 2006). Furthermore, to our knowledge, no study has tested thoroughly how incubation temperature affects thermal growth performance at later life stages.

Field studies on teleost fishes have revealed some evidence for the countergradient hypothesis, in particular, in studies on salmonids (Jensen et al. 2000, Finstad et al. 2004, Nicola & Almodóvar 2004). On the other hand, recent experimental studies have not supported either of the first 2 hypotheses (Forseth et al. 2001, 2009, Jonsson et al. 2001, Larsson et al. 2005), but leave the third possibility open. Circumstantial support for the third hypothesis was also given by a 25 yr long monitoring of the production of the anadromus salmonid Atlantic salmon *Salmo salar* L. in the River Imsa, Norway. In this river, Atlantic salmon juveniles grow better and are younger at seaward migration in years when the river is relatively warm during the embryonic development in winter compared with years when the water is colder in the incubation period. The difference is independent of the water temperature in the subsequent summer season (Jonsson et al. 2005). Thus, there is good reason for experimentally testing whether fish developed from eggs incubated under different thermal conditions exhibited different thermal performance curves. Based on previous field observations, we expected that groups of eggs incubated in relatively warm water would produce better-growing juveniles than conspecific groups developed in colder water. We used 2 incubation temperatures, designated natural and heated water. The warm water group was reared in heated water until the start of exogenous feeding. Half of the group incubated in natural, unheated water was transferred to heated water

right after hatching. The rest of the fish incubated in natural water were reared in unheated water until the start of exogenous feeding. Juvenile growth performances of these 3 groups were then tested at 8 different temperature regimes.

MATERIALS AND METHODS

The experiment was conducted at the Norwegian Institute for Nature (NINA) Research Station, Ims, in Southwestern Norway (59° N, 6° E) from November 2010 to September 2011. The fish used in the experiment were offspring of adult Atlantic salmon collected when returning from the sea to the River Imsa (59° N, 6° E). Eggs were collected from 24 females and fertilized with 2 males for each female (29 October 2010). Each family group was then split in 3 parts for use in the 3 different treatments. Family groups were kept separated until onset of exogenous feeding. During incubation, eggs were maintained in natural, unheated (2.6°C ± 0.4 SD) or heated (7.2°C ± 0.6 SD) River Imsa water (Fig. 1). The warm water treatment group was retained in heated water until the start of exogenous feeding (31 March 2011). At the time of hatching in the natural temperature treatment (9 March 2011), half of these fish were transferred to heated water, until natural water temperatures approached the heated ones, and the heating system was turned off (Fig. 1). The 3 different treatments are hereafter termed heated or natural tem-
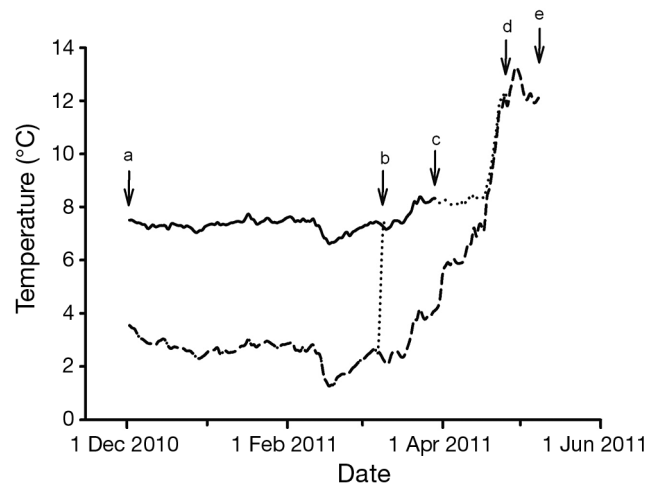

Fig. 1. *Salmo salar.* Water temperature during the early life history of Atlantic salmon kept in heated (——), mixed (· · ·) and natural (–·–·–) incubation temperature treatments. Arrows indicate date of (a) fertilization, (b) transfer of the mixed treatment from natural to heated temperatures, and start of exogenous feeding for (c) heated, (d) mixed and (e) natural treatment fish

perature treatments for the groups developed at elevated or natural water temperatures, respectively, from incubation to the start of exogenous feeding and mixed water temperature treatments for fish transferred from natural to heated water at the time of hatching.

After the start of exogenous feeding and until the start of the growth performance measurements, the fish were reared at natural water temperatures (range 6.5 to 20.0°C). The growth performance experiment was run at 8 temperatures (range 6 to 24°C) in 2 batches, from 16 September to 7 October (10, 14, 18, 21 and 24°C) and from 7 to 27 October (6, 8 and 16°C). During the growth performance measurement, the fish were kept in tanks that were 45 × 45 cm and 60 cm deep. The tanks had a water level of 30 cm, a water flow of 2 l min^{-1}, and a surface light intensity of approximately 70 lx during daytime (12 h light: 12 h dark cycle). No fish was used more than once. The setup was designed so that 2 replicates of each incubation temperature were run simultaneously for each experimental temperature. Ten individually marked fish (Alcian blue in fins and adipose fin clipping) were used in each tank. Experimental units were randomly distributed within each temperature regime to avoid systematic tank effects. Oxygen saturation was always close to 100% during the experiment. The fish were fed to satiation with granulated fish food administered from automatic feeders. Each fish was weighted (precision: ± 0.01 g) at the beginning and at the end of the experiment after the fish had been starved for approximately 24 h. The experiments lasted for 20 d each. Fish that died during the experiment (19 out of 480) were replaced by similarly sized fish to maintain densities at 10 fish per tank, but the replacement fish were not included in the results. The setup of the growth performance experiments followed a well-documented and standardized protocol (Jonsson et al. 2001, Finstad et al. 2004, 2011, Larsson et al. 2005, Forseth et al. 2009). Mean mass (±SD) of the fish at start of the first growth experiment run was 6.2 ± 1.2, 9.0 ± 1.4, and 12.1 ± 2.2 g for natural, mixed and heated incubation temperatures, respectively, and 9.4 ± 2.4, 11.6 ± 2.5, and 14.7 ± 3.1 g for the second.

We tested for effects of incubation temperature treatment on growth rate using standarized growth (Ω) according to Ostrovsky (1995):

$$\Omega = (M_t^b - M_0^b) \times \frac{100}{(b \times t)} \qquad (1)$$

where M_t and M_0 are the respective body masses at the end and beginning of the experiment, t is the

duration of the experiment in days and b is the allometric mass exponent for the relationship between specific growth rate and body mass, which was set to 0.31 (Elliott et al. 1995). Ω effectively eliminates the effects on growth rates of differences in initial body sizes (Sigourney et al. 2008, Forseth et al. 2010), and there was no effect of individual mass at the start of the growth experiment on standardized growth rates ($F_{1,459} = 1.81$, p = 0.178). Within each incubation treatment temperature, we fitted the predicted curve for temperature scaling of mass standardized growth as:

$$\Omega = d(T - T_L) \times (1 - e^{g(T - T_U)}) \qquad (2)$$

where T (°C) is the experimental temperature, T_L and T_U are the estimated lower and upper temperature for growth, and d and g are constants. Following Forseth et al. (2001) and Jonsson et al. (2001), only data for the 3 fastest growing quartiles within each tank were used in further analyses in order to avoid bias due to social interactions and resulting growth depression common for salmonids in tank experiments. Parameters for Eq. (2) were estimated with non-linear least-squares regression using the nls function in R version 2.10.1 (R Development Core Team 2010). We initially tested for tank effects by including tank as a random effect using the non-linear mixed effect (nlme) procedure in the nlme library of R (Pinheiro et al. 2009). Inclusion of tank as a random effect did not improve the model because the Akaike's information criterion (AIC) of models with random effects was higher than those for models without.

The maximum growth (c) of the different incubation-temperature treatments was inferred as the mass standardized growth at the optimal temperature (T_M), i.e. the height of the growth curve, where optimal temperature for growth can be expressed by solving the following (Jonsson et al. 2001):

$$\ln[1 + g(T_M - T_L)] = -g(T_M - T_U) \qquad (3)$$

Overall differences between incubation temperature treatments on growth performance were explored by analysis of variance (ANOVA) of the residuals from a common growth model fitted for fish from all incubation temperature treatment groups (Eq. 2). Differences among treatments in thermal scaling of growth and maximum growth were explored by evaluating parameter values and 95% confidence intervals from growth models fitted for each treatment group. Confidence intervals were estimated using bootstrapping (10 000 permutations) (Efron & Tibshirani 1993).

RESULTS

Growth rate differed among juvenile Atlantic salmon experiencing differences in incubation temperature (Fig. 2). Judged from group differences between residuals from a common growth model, there were overall significant differences in growth among the incubation temperature treatments (ANOVA, $F_{2,323}$ = 15.35, p < 0.001). Juvenile salmon experiencing heated temperatures during the whole incubation period grew faster overall than the 2 other treatment groups (Table 1), whereas there were only marginal differences in overall growth rate between the natural and mixed incubation temperature treatments.

The thermal scaling of growth did not differ significantly between the treatment groups (Table 2). The estimated lower thermal limit for growth (T_L) was 6.82, 7.70 and 6.76°C for natural, mixed and heated incubation temperatures, respectively. The estimated upper thermal limit for growth was 24.80, 24.43 and 25.15°C for natural, mixed and heated incubation temperatures, respectively. As judged from confidence intervals of the estimated coefficients, there was no significant difference in the thermal scaling of growth between treatment groups.

The maximum growth rate (height of the growth curve, c) was significantly higher in the heated compared to the natural and mixed incubation temperature treatments, as judged from the coefficients and bootstrapped confidence intervals (Table 2, Fig. 2). However, there were no differences in the maximum growth rates of fish reared in the natural and mixed incubation temperature treatment (Table 2). As a result, the heated incubation temperature group grew faster from temperatures of approximately 17°C upwards, reaching an optimal temperature for growth (T_M) at 19.73°C. This was slightly higher than those of the natural and mixed temperature treatments (17.90 and 19.20°C, respectively) and, as judged from the overlap in confidence intervals, not significant (Table 2). Also, when considering uncertainties in the estimated coefficients, there were only
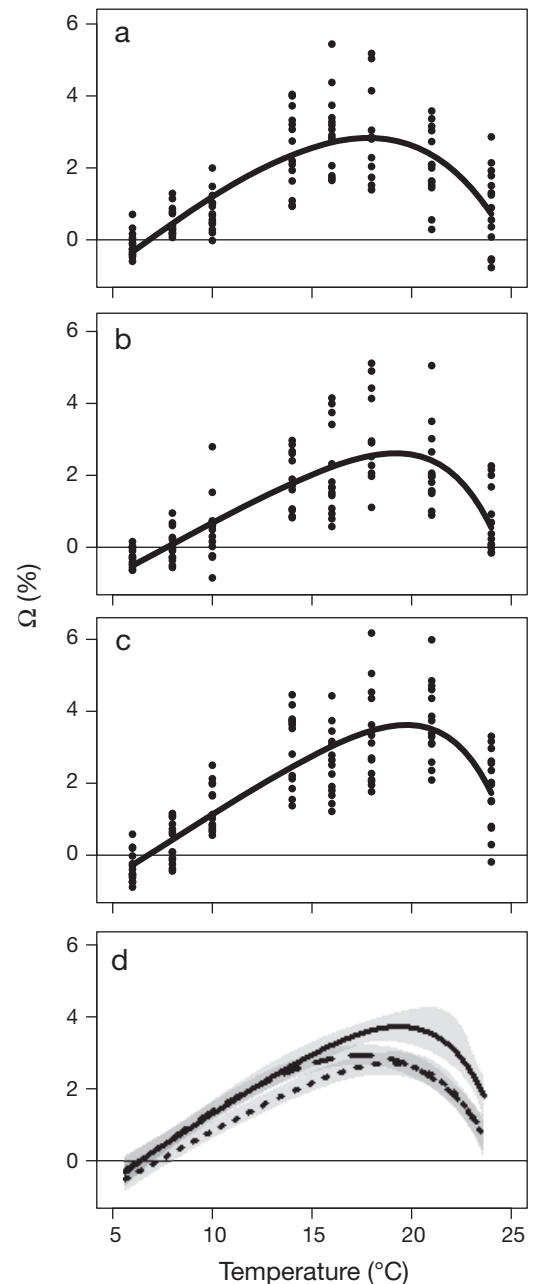

Fig. 2. *Salmo salar.* Temperature scaling of body size standardized growth (Ω, %) for juvenile Atlantic salmon kept at (a) natural, (b) mixed and (c) heated incubation temperatures (°C, cf. Fig. 1). Lines are fitted thermal growth models (Eq. 2, see Table 2 for parameter values); dots indicate individuals. (d) Estimated growth models from natural (---), mixed (•••) and heated (——) incubation temperatures are superimposed on each other and given with 95% confidence intervals (grey shading). Horizontal line indicates zero growth

minor differences in growth along the tested temperature gradient for natural and mixed incubation temperature treatments (Fig. 2d).

Table 1. *Salmo salar.* Tukey multiple comparisons of means for analysis of variance (ANOVA) with residuals from common growth model fitted for fish from all incubation temperature treatment groups as the response and treatment (natural, mixed and heated water temperatures) as the factor

Comparison	Mean difference	95% CI	p
Mixed vs. natural	−0.31	−0.61, −0.01	0.044
Heated vs. natural	0.40	0.09, 0.70	0.005
Heated vs. mixed	0.71	0.40, 1.01	<0.001

Table 2. *Salmo salar.* Estimated model parameters (±95% confidence intervals) for the thermal scaling of growth as determined by the standardized mass specific growth rate, Ω, in Eq. (1) for Atlantic salmon juveniles reared at natural, mixed (natural until hatching and heated until start of exogenous feeding) and heated incubation temperatures (Fig. 1). See Eqs. (2) and (3) for model used to estimate these parameters. T_L: estimated lower temperature for growth, T_M: optimal temperature for growth; T_U: estimated upper temperature for growth, d: constant, g: constant, c: maximum growth (height of the thermal growth curve)

Treatment	d	g	c	T_L	T_M	T_U	R^2
Natural	0.44 (0.31–0.64)	0.12 (0.07–0.23)	2.84 (2.57–3.11)	6.82 (5.83–7.51)	17.90 (17.12–18.74)	24.80 (24.22–25.57)	0.68
Mixed	0.30 (0.24–0.40)	0.27 (0.15–0.45)	2.61 (2.32–2.93)	7.70 (6.59–8.53)	19.20 (18.28–20.12)	24.43 (24.04–25.15)	0.62
Heated	0.35 (0.27–0.72)	0.28 (0.06–0.97)	3.64 (3.23–4.15)	6.76 (5.56–7.61)	19.76 (18.30–21.49)	25.15 (24.29–27.25)	0.67

DISCUSSION

Temperature has profound effects on the development of ectotherms during embryogenesis. This is the period when cells and tissues are differentiated and the embryo's organs and main external features begin to take form. For instance, meristic characters such as numbers of vertebrae and fin rays of teleosts are influenced by temperature during the embryonic period (Tåning 1952, McDowall 2008). Temperature also regulates the time of myogenesis, composition of the sub-cellular organelles and patterns of gene expression. Also, the number and size of white muscle fibres and the shape of the heart depend on temperature during early development, critical to longer-term muscle growth. Muscle changes induced during this period of plasticity appear irreversible (Johnston 2006, Albokhadaim et al. 2007, Jonsson & Jonsson 2011). Even the sex determination of salmonids is affected by temperature during early ontogenesis (Craig et al. 1996). There is no similar period in life when the ambient temperature has a similar pervasive effect on the later functioning of organisms.

In line with this, our results support the hypothesis (see 'Introduction') that thermal conditions experienced by incubating embryos affect later growth performance, as earlier observed for reptiles (Booth 2006). Juvenile salmon incubated in untreated River Imsa water grew less well in water warmer than 17°C than those incubated in heated River Imsa water. We know of no similar study showing a prolonged growth response to embryonic temperature from a developed teleost fish. Earlier, Martell et al. (2005) reported that temperature during embryogenesis influenced the subsequent larval growth of haddock *Melanogrammus aeglefinus*. Also, Korwin-Kossakowski (2008) reported that larval growth of common carp *Cyprinus carpio* was enhanced during the first 14 d of

exogenous feeding as a consequence of increased temperature between hatching and time of first feeding. The latter author assumed that a shorter and less energy costly embryonic period might promote later growth performance. Álvarez et al. (2006), however, demonstrated that the standard metabolic rate of brown trout *Salmo trutta* changed in response to the temperature experienced by yolk feeding larvae. They assumed that this was a result of countergradient adaptation, but this might also be a phenotypically plastic response as observed in the present study.

Rungruangsak-Torrissen et al. (1998) found different trypsin isozymes in groups of Atlantic salmon hatched at 6° and 10°C. Trypsin is a key digestive protease, which is sensitive to environmental change and influences feed utilization and growth during the entire life cycle (Rungruangsak-Torrissen & Male 2000). The various trypsin isozyme variants influence maintenance ration and the capacity for protein synthesis in white muscle with effects on growth, size and other life history variables. Rungruangsak-Torrissen et al. (1998) assumed that their incubation groups were genetically different, but this may have been a phenotypically plastic response, as we observed in the present experiment. If so, their biochemical findings may give the physiological mechanism for this plasticity. The genetic mechanism for such flexible trypsin production is unknown, but Jump & Clark (1999) maintained that environmental factors may interact with the genome and allow cells to adjust to an on/off switch gene expression. Sainz et al. (2005), on the other hand, concluded from a study of isotrypsin patterns that the regulation was quantitative not qualitative and that changes in trypsin activity and in trypsin mRNA by internal and external stimuli must be related to changes in the rate of synthesis of the established isoenzymes. In any case, trypsin regulation is one possible mecha-

nism for the observed growth trajectories influenced by the temperature experienced by the embryos.

The River Imsa is relatively warm for Norway (e.g. Jonsson et al. 2001), but we expect that the observed phenotypic relationship between increased embryonic temperature and later growth performance is general and also holds for conspecific populations inhabiting colder systems. Furthermore, it may also hold for other teleost species. For instance, Atlantic cod *Gadus morhua* reared from young cod caught in the warmer Clyde Sea on the west coast of Scotland grew faster than cod from St Andrews Bay when the young were brought together and reared larger under similar controlled experimental conditions (Harrald et al. 2010). The authors assumed that this was the result of genetic adaptation among cod from different areas, but a phenotypic response to early temperature, such as shown in the present study, is a possible alternative explanation since St Andrews Bay is relatively cold compared with the Clyde Sea.

A plastic response to local environments may function as a pre-adaptation to expected conditions the fish meet after hatching. Aquatic production increases with water temperature, and fish which are incubated in a relatively warm habitat may expect to encounter relatively rich feeding opportunities and keen competition as juveniles in the river, increasing the selective premium on fast growth. On the other hand, in a cold environment, this is less advantageous not only because of poorer growth opportunities, but also because faster growth has increased costs in the form of increased resource demands and higher mortality (Mangel 2003, Metcalfe & Monaghen 2003, Sundt-Hansen et al. 2009).

Adapting growth rate to expected environmental conditions may give the fish a selective advantage, i.e. adaptive plasticity (cf. Gotthard & Nylin 1995, Ghalambor et al. 2007). Although the present experiment does not test for among-population variation in incubation temperature-induced growth plasticity, one can speculate that local adaptations may arise as a response to differences in the seasonal temperature regime. Such a potential mechanism may further explain contrasting findings of countergradient variation or local thermal adaptation in growth from common environment experiments (Forseth et al. 2010, Jonsson & Jonsson 2011). Typically, such experiments rear embryos whose parental generations originated from cold and warm natal environments at the same temperature. Embryos from a cold environment may then experience this as elevated temperatures compared to their natal environment and show elevated growth at later life history stages and vice versa for embryos originating from warm natal environments.

This juvenile growth response to thermal conditions during embryogenesis is relevant in the context of climate change. Future temperature is expected to increase, at least during the 21st century. The main scenario in the Atlantic region is milder, wetter and stormier winters. Warming is expected to be greatest over land and at high northern latitudes (IPCC 2007). During the 20th century, stream temperatures increased by 1° to 3°C in Europe (Daufresne et al. 2004, Webb & Nobilis 2007), and the current winter temperature in the River Imsa is between 2° and 4°C most years and may increase another 3°C during this century (Hanssen-Bauer et al. 2003), reaching up to ca. 7°C as in the present experiment. Such an increase will have severe consequences for juvenile growth, and age and size at seaward smolt migration. In a recent field study in the River Imsa, Atlantic salmon offspring hatched from eggs incubated in relatively warm winters were found to exhibit faster juvenile growth than offspring hatched from eggs incubated during winters when the river water was colder (Jonsson et al. 2005). As a result, fish from eggs incubated in relatively warm winters tended to develop faster and migrate to sea younger than conspecifics incubated in colder water. Young emigrating salmon are usually relatively small, which affects the subsequent marine survival rate, age at maturity and thus the year-class production. This may be one of the reasons why the survival rate of Atlantic salmon in the River Imsa has decreased in recent years (Jonsson & Jonsson 2004). This latter contention is based on the observation that sea-survival of anadromous brown trout is relatively poor in years with relatively high winter temperatures, causing the fish to move to sea early in spring when the sea is relatively cold (Jonsson & Jonsson 2009). A similar relationship between time of migration and water temperature holds for Atlantic salmon (Jonsson & Ruud-Hansen 1985). Furthermore, Skilbrei (1989) reported that fast-developing Atlantic salmon tended to attain maturity younger, meaning that the adults were relatively small, which has been the trend in several European rivers during recent years (Jonsson & Jonsson 2004, Todd et al. 2008).

In all, water temperatures experienced by salmon embryos influence later growth performance, and this norm of reaction is probably more widespread among fishes and does not affect salmonids only. We also expect that temperatures experienced by the embryos influence more characteristics than metabolic and growth performances, as has been already found for reptiles.

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